

PRELIMINARY DESCRIPTION OF COELOPHYSOIDS (DINOSAURIA:THEROPODA) FROM THE UPPER TRIASSIC (REVUELTIAN:EARLY-MID NORIAN) SNYDER QUARRY, NORTH-CENTRAL NEW MEXICO

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Abstract—The Upper Triassic Snyder quarry is the second-most productive theropod locality in the Chinle Group. Skull and postcranial elements, particularly tibiae, collected from the Snyder quarry during the last three field seasons demonstrate the presence of at least four individuals of two taxa. The smaller theropod strongly resembles, but is distinct from, the holotype of *Eucoelophysis baldwini* Sullivan and Lucas and represents either a sexual dimorph or, more likely, a new species of *Eucoelophysis*. The larger theropod is represented by a single, incomplete fused tibia-fibula-astragalus-calcaneum. Most striking about this taxon is the proximal fusion of the tibia and fibula. These theropods are a small fraction of a rich and diverse assemblage of Upper Triassic vertebrates and invertebrates from the most productive Chinle Group vertebrate fossil assemblage discovered in the last 50 years.

INTRODUCTION

In 1998, Mark Snyder of Del Mar, California, discovered a spectacular assemblage of fossil vertebrates in the badlands of the Upper Triassic Petrified Forest Formation near Ghost Ranch, north-central New Mexico (Fig. 1). Since that time, we have made extensive excavations at this locality and collected a diverse fauna of both vertebrates and invertebrates. In this paper, we briefly describe the geology of the site, list the known fauna, and preliminarily describe the theropods of that fauna. In this paper, NMMNH = New Mexico Museum of Natural History and Science, Albuquerque; and UCMP = University of California Museum of Paleontology, Berkeley.

GEOLOGY

The Snyder quarry (NMMNH locality 3845) is stratigraphically high in the Petrified Forest Formation of the Chinle Group (Fig. 2). The Petrified Forest Formation in north-central New Mexico is stratigraphically equivalent to the Painted Desert Member of the Petrified Forest Formation in west-central New Mexico and Arizona and the Bull Canyon Formation in east-central New Mexico and West Texas (Lucas, 1993, 1997). Thus, the Snyder quarry is broadly correlative to the upper faunas of the Petrified Forest National Park (e.g., Murry and Long, 1989; Hunt and Lucas, 1995), Bull Canyon Formation faunas in eastern New Mexico (Hunt, 1994) and the Post quarry in Texas (Small, 1989). The Snyder quarry lies 28.5 m below the contact of the Petrified Forest Formation with the overlying Rock Point Formation and 64 m below the Middle Jurassic Entrada Sandstone (Fig. 2). This stratigraphic interval is roughly correlative to both the famous Canjilon quarry (Lucas and Hunt, 1992) and the type locality of *Eucoelophysis*, which appears to approximate the horizon collected by D. Baldwin for E.D. Cope (Sullivan et al., 1996; Sullivan and Lucas, 1999).

The Snyder quarry consists of three primary fossiliferous horizons in a series of fining-upwards sequences in a prominent grayish-green band of sediment (Fig. 2). Each of these sequences generally consists of a basal pebble conglomerate that fines up through a very thin (<5 cm) muddy sandstone/sandy mudstone (wacke) into a 1-1.5-m-thick laminated mudstone-dominated bed. The vast majority of the fossil bones, including all of the dinosaur

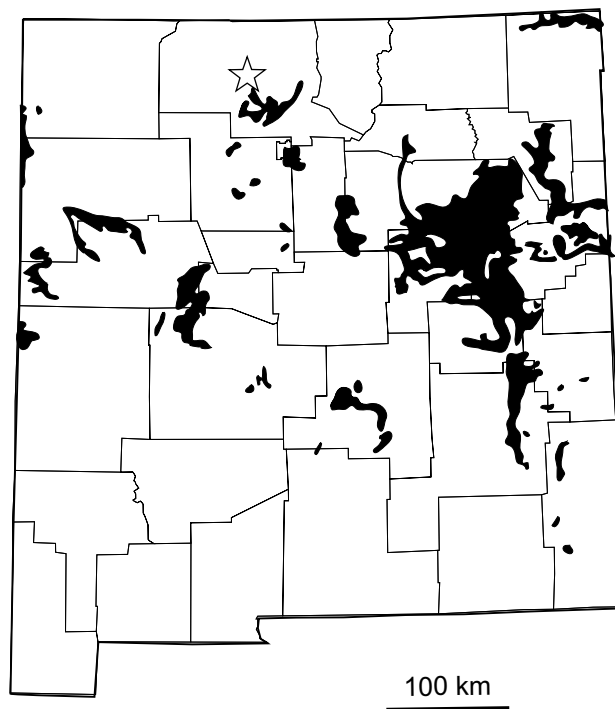


FIGURE 1. Index map showing Triassic outcrops and the location of the Snyder quarry in New Mexico.

material described here, are found in the basal sequence, in either the mudstone-pebble conglomerate or the immediately overlying sandstone-wacke interval (base of unit 2 in Figure 2). This interval is sometimes referred to in NMMNH records as locality 3845-1. Fossils from the other two fining-upwards cycles are designated as locality 3845-2 and locality 3845-3, respectively. Some theropod fossils, principally vertebrae and possible metapodials, occur in these higher conglomeratic layers, but this material is isolated and, quite possibly, reworked from the lower levels. One of us (KEZ) is undertaking a detailed study of the taphonomy of the site, which will explore the issues of bonebed geology and formation in greater detail.

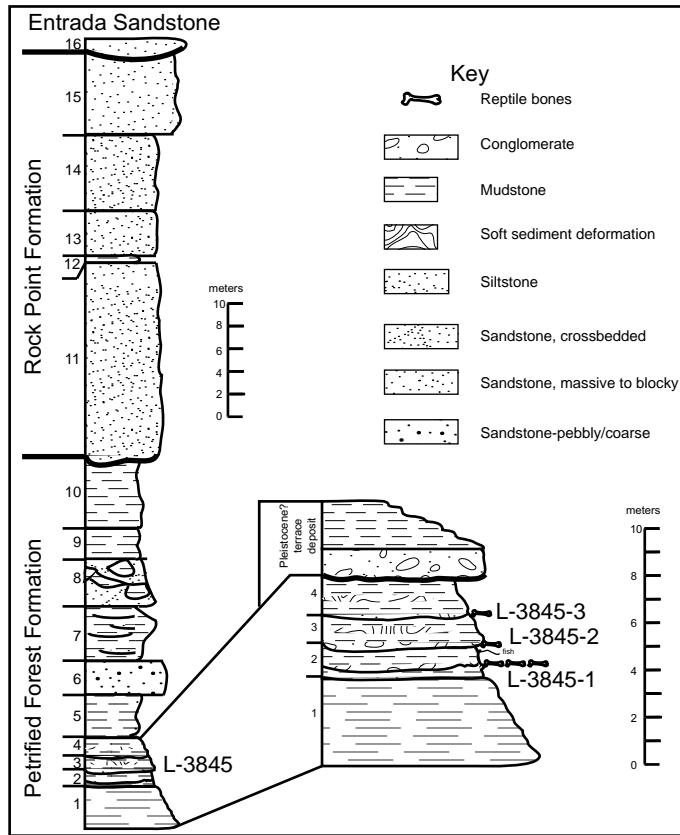


FIGURE 2. Measured sections showing the stratigraphic position of the Snyder quarry, NMMNH locality 3845.

Generally, most of the bones from the lower level (3845-1) are loosely associated, but they are not articulated. However, at least half of the theropod specimens are much more closely associated, with some elements articulated. Thus, while the theropod specimens we discuss below are given different specimen numbers in the NMMNH catalog, they probably only pertain to a few individuals, possibly as few as four.

THE FAUNA

The bonebed at the main level of the Snyder quarry (3845-1) is extremely rich. Additionally, the overlying layers (3845-2, 3845-3) yield a number of more isolated vertebrate remains as well as some invertebrates. To date, the invertebrate fauna consists of a conchostracan from the level of the main bonebed, a bank of unionid bivalves from the mudstone-pebble interval of the third conglomerate, and a decapod crustacean that was probably derived from immediately above the main bonebed (Rinehart et al., 1999).

The vertebrate fauna from the quarry includes semionotid and colobodontid fish, very rare metoposaurid amphibians, a diverse suite of archosaurs, including phytosaurs, aetosaurs, and theropod dinosaurs, and possible cynodonts. An incomplete articulated semionotid fish was recovered from mudstones in the second fining-upward sequence. Additional semionotid scales are commonly found in screenwash concentrate of the matrix from the principal bonebed. Screenwashing has also yielded at least two incomplete colobodontid tooth plates.

At this time, metoposaurid fossils from the Snyder quarry are limited to an isolated centrum and several labyrinthodont teeth. Although these are not, strictly speaking, determinate, they

probably pertain to *Buettneria*, which is the only large temnospondyl known from this stratigraphic interval in the Chinle (Hunt, 1993). The centrum is both too large and not sufficiently elongate to justify referral to *Apachesaurus*, which is normally more abundant in the upper Chinle than *Buettneria*.

Phytosaurs dominate the fauna both in terms of total number of elements preserved and total number of individuals represented. Phytosaur postcrania, particularly vertebrae and proximal limb bones, are common at the quarry. More striking, however, is the wealth of cranial material. To date we have collected ten phytosaur skulls and large, unopened jackets probably contain two more. Only one of these skulls is completely prepared at this time, but this and field observations indicate that these phytosaurs all have elongate squamosals and supratemporal fenestrae depressed below the level of the skull roof, characteristics typical of *Pseudopalatus*-grade phytosaurs *sensu* Ballew (1989). At least some of the skulls exhibit particularly bulbous narial crests. Although only the one skull is completely prepared, comparison with the UCMP collections from the nearby Canjilon quarry (UCMP locality V2816) suggests that most, if not all, of these phytosaurs are assignable to *Pseudopalatus*, probably *P. buceros sensu* Ballew (1989). Note that this is a preliminary identification because, in spite of three recently published taxonomic schemes (Ballew, 1989; Hunt, 1994; Long and Murry, 1995), significant taxonomic problems remain with numerous phytosaur taxa, including *Pseudopalatus*.

In addition to the abundant phytosaurs, aetosaur fossils are common at the quarry. To date, aetosaur scutes are by far the most common aetosaur fossils from the site, with very few postcrania and no skull or jaw material known at this time. Fortunately, aetosaur paramedian (dorsal) and lateral scutes are generically diagnostic (Heckert and Lucas, 2000a, and sources cited therein). Aetosaur scutes from the Snyder quarry include numerous scattered scutes of *Desmatosuchus*, which marks the stratigraphically highest known occurrence of that taxon (Zeigler et al., 2000). Additionally, we have recovered numerous associated to partially articulated scutes of the aetosaur *Typothorax coccinarum*. Thus far, most of the *Typothorax* fossils were found in a relatively small area, whereas the *Desmatosuchus* scutes occur throughout the quarry.

Phytosaurs and aetosaurs dominate the fauna. To date, no definitive rauisuchian or sphenosuchian fossils have been identified in the recovered material, although a *Hesperosuchus*-like scute was collected this year. The remaining archosaurs are all theropod dinosaurs, which we discuss in greater detail below.

The only evidence of other amniote groups consists of a distal left humerus. This small (under 5 cm reconstructed length) bone possesses two offset condyles in the middle of a broad, elliptical sheet of bone. It superficially resembles the distal humeri of both cynodonts and some specialized lepidosauromorphs. We tentatively identify this element as a ?cynodont.

Theropods

Theropod fossils at the Snyder quarry are, by Chinle standards, abundant and well preserved. Two taxa, one considerably larger than the other, are represented. The majority of the theropod fossils pertain to the smaller morphotype and include an incomplete skull, lower jaws, and two articulated cervical vertebrae (Fig. 3A), a dorsal vertebra, an incomplete sacrum, an incomplete left scapulocoracoid, fragmentary right ilium (Fig. 3C), nearly complete right ischium (Fig. 3B), two femora, three tibiae, an astragalus, and numerous metapodials, phalanges, and ribs. All of the limb bones are hollow, and are preserved with thick calcite infilling surrounded by the comparably thin bone walls of the limb shafts. We briefly and preliminarily describe these theropod fossils and discuss their affinities here.

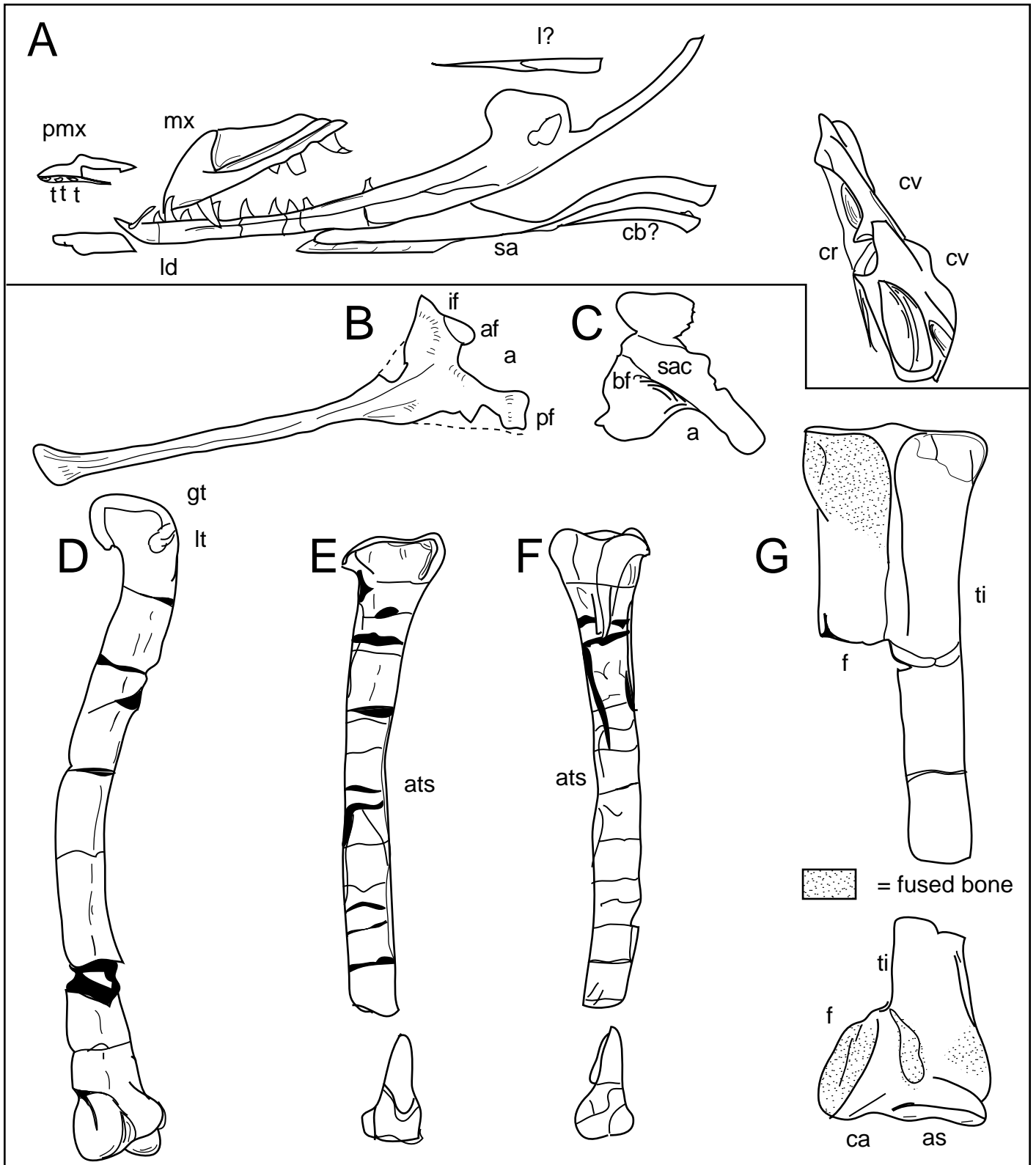


FIGURE 3. Coelophysoid theropods from the Snyder quarry. **A**, incomplete skull, lower jaws, and articulated cervical vertebrae in left lateral view; **B**, incomplete right ischium in lateral view; **C**, incomplete right ilium in lateral view; **D** right femur in posterior view; **E-F**, nearly complete, slightly crushed left tibia in **E**, anterior and **F**, posterior views; **G**, large coelophysoid, incomplete fused tibia-fibula-astragalus-calcaneum. All are approximately 75% actual size. Abbreviations: **a** = acetabulum; **af** = acetabular facet; **as** = astragalus; **ats** = appressed tibial surface; **bf** = brevis fossa; **ca** = calcaneum; **cb?** = ceratobranchial?; **cr** = cervical rib; **cv** = cervical vertebra; **f** = fibula; **gt** = greater trochanter; **if** = iliac facet; **l?** left lachrymal?; **mx** = maxilla; **pmx** = premaxilla; **sa** = surangular; **sac** = supra-acetabular crest; **t** = tooth; **ti** = tibia.

Description

Skull—The preserved skull material includes a left premaxilla and maxilla and a possible left lachrymal (Fig. 3A). The premaxilla is slightly disarticulated and rotated so that it is viewed occlusally in Figure 3A. Were it rotated back into position, there would be a distinct subnarial gap, the distinctive trait of most ceratosaurs (Rowe and Gauthier, 1989). The anterior margin of the antorbital fenestra is bounded by the dorso-posteriorly projecting ascending process of the maxilla, as is typical of coelophysids. The lachrymal? is only partially exposed in medial view and thus reveals little diagnostic information.

Lower jaw—Both the right and left dentaries are preserved, together with incomplete angulars and surangulars, a left splenial and a possible ceratobranchial. The dentaries are slender and elongate. The surangular is moderately deep and appears somewhat more robust than that of *Coelophysis* or *Syntarsus*.

Teeth—There are four very small teeth or alveoli visible in the premaxilla. These teeth, anterior to the subnarial gap, follow the pattern observed in *Syntarsus* (Raath, 1977, 1990) and *Coelophysis* (Colbert, 1989, 1990), where premaxillary teeth are much smaller than maxillary teeth or most dentary teeth. The maxilla contains at least 10 teeth or visible alveoli, and the left dentary nine, although matrix conceals much of the tooth-bearing portions of these bones. Total tooth counts were probably much closer to 25 teeth per row (Paul, 1993). The teeth are all laterally compressed and strongly recurved. The maxillary and dentary teeth are approximately subequal in size, but both are considerably larger than the tiny premaxillary teeth. This is the oldest occurrence of marked heterodonty in theropods.

Vertebral column—Two cervical vertebrae were found articulated with the skull (Fig. 3A). These may correspond to the third or fourth (or fourth and fifth) cervicals. They are low, elongate, and deeply pleurocoelous with greatly reduced neural spines. These and another cervical vertebra all possess elongate, extraordinarily delicate, cervical ribs.

The best-preserved dorsal vertebra is amphicoelous, taller, and more robust than the cervicals. The sacrum consists of five fused vertebrae. The first four of these are thoroughly fused across both their articular surfaces and their neural processes. The last sacral is a sacro-caudal and is less strongly fused across its articular facets.

Scapulocoracoid—The incomplete left scapulocoracoid lacks approximately half of the scapular blade but is otherwise nearly complete. In lateral view, the scapula is more symmetrical at the level of the glenoid (anterior projection = posterior projection of the acromion) than illustrated for *Coelophysis* (Colbert, 1989) or *Syntarsus* (Raath, 1977; Tykoski, 1998). This element is somewhat similar to *Eucoelophysis* (Sullivan and Lucas, 1999), but the glenoid is more arcuate and the scapula as a whole more gracile than that taxon, although this may be an artifact of the larger size of the holotype of *Eucoelophysis*. The coracoid possesses a strong glenoid pillar and is likewise more expanded than illustrated in the other coelophysoids.

Ilium—Only a very fragmentary right ilium is known (Fig. 3C). However, this ilium and the articulated right ischium (Fig. 3B) demonstrate the presence of a very large, entirely open acetabulum. A prominent supra-acetabular crest curves laterally over the acetabulum and the anterior margin of the brevis fossa. Both the ischial and pubic pedicles are preserved and are roughly subequal in length.

Ischium—The ischium is straight and elongate, with only a modest distal swelling for the ischial boot. The dorsally projecting iliac and acetabular facets are well-developed, as is the anteriorly projecting pubic process.

Femur—Right and left femora were found in close association with other hind limb elements in 1998. The femora are marked by a medially offset head that is slightly “hooked” in anterior or posterior view (Fig. 3D). This is more strongly developed than in *Eucoelophysis* or illustrated by Colbert (1989) for *Coelophysis*, yet less strong than that seen in *Syntarsus rhodesiensis*. The femora lack the proximal groove or sulcus of *Eucoelophysis*. The anterior or lesser trochanter is a prominent subtriangular ridge. Although this differs from the condition in *Eucoelophysis*, it corresponds to the “robust” morph of *Syntarsus* (Raath, 1977; Tykoski, 1998), whereas *Eucoelophysis* corresponds to the gracile morph (Sullivan and Lucas, 1999).

Tibia—There are portions of three small coelophysoid left tibiae from the Snyder quarry. One is essentially complete, a second nearly so (Fig. 3E-F) and a third consists solely of the proximal end and was found beneath the ilium and ischium. The most striking feature of the tibia is the strongly appressed surface that was held in contact with the fibula. This condition exactly matches that of *Eucoelophysis* and differs from *Syntarsus* and *Coelophysis*, although the articulated nature of specimens of the latter makes this condition difficult to assess in the Ghost Ranch theropod sample (Downs, 2000). There is no evidence of fusion of the tibiae to more distal elements on either specimen for which a distal tibia is preserved. There is, however, a marked hollow in the base of the tibia to accept the ascending process of the astragalus.

Fibula—Two incomplete fibulae are known. Relative to the tibiae they are greatly reduced and, as described above, fit against an appressed surface on the tibia. There is no evidence of fusion of the fibula to the tibia or to distal elements.

Other elements—To date, we have recovered numerous metapodials and phalanges, including an astragalus and at least one ungual phalanx. Pending further cleaning and preparation these will be detailed in a later work, but we note here that the phalanges and metapodials are gracile, with greatly reduced shafts relative to their articular ends.

Larger coelophysoid—Preparation of the third jacket removed from the quarry yielded a large, nearly complete tibia-fibula-astragalus-calcaneum. The most striking aspect of this bone is the fusion not only of the distal tibia and fibula to the astragalus and calcaneum, but the complete fusion of the proximal fibula to the tibia (Fig. 3G). Although this extensive fusion has resulted in large areas of slightly rugose bone surfaces, this texture is still relatively smooth and not obviously pathologic (D. Tanke and B. Rothschild, pers. comm.). Furthermore, the shafts of the tibia and fibula are neither fused nor appressed. The former condition precludes assignment to *Eucoelophysis*, and the latter provides additional argument against a pathological origin for the fused bone. The tibia and fibula are hollow and filled with calcite. The prominent ascending process of the astragalus is still distinct beneath the fused bone surface, also supporting a theropod identification for these bones, and the fusion, if not pathologic, is a feature typical of derived ceratosaurs.

Affinities

The subnarial gap, heterodont premaxilla, gracile limb bones, and numerous other features all support assignment of the smaller theropod to the Ceratosauria and, more specifically, to the Coelophysoidea. However, the coelophysoid taxa *Eucoelophysis*, *Coelophysis*, and *Syntarsus* are exceedingly similar in many details of the skeleton, so much so that some authors have stated, either explicitly (Paul, 1993) or implicitly (Downs, 2000), that all of these taxa should be assigned to a single genus. Thus, while we have documented numerous differences between the Snyder quarry theropods and other coelophysoid taxa, we

take the conservative approach here and choose not to erect a new name. In general, the smaller coelophysoid most closely resembles *Eucoelophysis*, particularly in details of the scapulocoracoid, ischium, and tibia. Some of the differences between these theropods and *Eucoelophysis* may warrant erection of a new species, but many of these differences, particularly in the femur, could be sex-related, as posited by Raath (1977). Thus, we tentatively refer the smaller theropod to *Eucoelophysis* sp. The larger theropod is too fragmentary to identify with certainty, but this specimen certainly appears unique among ceratosaurs.

BIOSTRATIGRAPHY AND BIOCHRONOLOGY

Lucas and Hunt (1992) and Hunt and Lucas (1993) assigned the Petrified Forest Formation in the Chama Basin an early-mid Norian age. This conclusion was based on stratigraphic position and the presence of the aetosaur *Typothorax* and *Pseudopalatus*-grade phytosaurs in the Canjilon quarry. Lucas and Hunt (1993) erected a series of temporally successive land-vertebrate faunachrons (lvf—identical in concept to land-mammal “ages”), and assigned the time interval represented by the fauna with *Typothorax coccinarum* and *Pseudopalatus*-grade phytosaurs to the Revueltian lvf. The Revueltian lvf represents time from the early to approximate mid-Norian on the standard global chronostratigraphic timescale (Lucas, 1998), approximately 212–218 Ma (Kent et al., 1995). Given that both the phytosaur *Pseudopalatus* and the aetosaur *Typothorax coccinarum* occur at the Snyder quarry and at the correlative Canjilon quarry, and that both of these archosaurs are index taxa of the Revueltian land-vertebrate faunachron (Lucas, 1998), we confidently assign the Snyder quarry to the Revueltian lvf. Given the relatively high stratigraphic position of the Snyder quarry, closer to the Rock Point Formation than the underlying Poleo Sandstone, we anticipate that it is in strata deposited in the latter half of Revueltian time.

The fauna of the Snyder quarry corresponds almost exactly to that expected in Revueltian deposits (Lucas, 1998). The only aberrant taxon is *Desmatosuchus*. Although *Desmatosuchus* is known from the Revueltian, most of these occurrences are stratigraphically low in Revueltian strata, and *Desmatosuchus* is generally rare in Revueltian-age strata (Lucas and Heckert, 1996; Heckert and Lucas, 2000). Thus, *Desmatosuchus* from the Snyder quarry marks the stratigraphically highest occurrence of that taxon (Zeigler et al., 2000).

SIGNIFICANCE

The theropods from the Snyder quarry are important for several reasons: (1) dinosaurs are a relatively rare component of almost all Chinle faunas; (2) these theropods are some of the best-preserved early coelophysoids; (3) their stratigraphic position, roughly correlative to the type locality of *Eucoelophysis baldwini*, enhances our understanding of the superposition of Upper Triassic dinosaur faunas; and (4) all of these combine to improve our understanding of Late Triassic dinosaur evolution.

As mentioned previously, dinosaurs in general are a rare component of Chinle faunas. Although the theropods described here are numerically and volumetrically a relatively small component of the Snyder quarry fauna, the presence of four individual theropods of two taxa qualifies this as the second-most productive Chinle theropod site. Aside from the *Coelophysis* Lagerstätte, no other Chinle locality preserves either this diversity or number of theropod body fossils.

The Snyder quarry vertebrate fossils are, in general, exquisitely preserved. This is especially true of the coelophysoid theropods. Indeed, the coelophysoids present a taphonomic prob-

lem—how to preserve delicate elements such as the skull, cervical ribs, and pelvis of the coelophysoids in the same depositional regime that was transporting phytosaur skulls and postcrania? Regardless of the answer, the coelophysoid fossils from the Snyder quarry are the best preserved of any Chinle theropod fossils outside of the *Coelophysis* quarry.

The Chama basin in northern New Mexico is the only location in the Chinle Group with two clearly superposed theropod faunas. The lower fauna includes the type of *Eucoelophysis baldwini* and the Snyder quarry theropods, which we have amply demonstrated to be of Revueltian age. Overlying these theropods, in the Rock Point Formation, is the *Coelophysis* Lagerstätte, of younger, Apachean (latest Norian-Rhaetian?) age (see Lucas and Hunt [1992] and Sullivan et al. [1996] for detailed stratigraphy). Thus, material at the Snyder quarry, the type of *Eucoelophysis*, and at least some of Baldwin’s original material named *Coelophysis* by Cope are demonstrably older than the *Coelophysis* material discovered by G.H. Whitaker for E.H. Colbert at Ghost Ranch.

The stratigraphic range of coelophysoids is now well established and reasonably well constrained, facilitating a better understanding of the early evolution of the dinosaurs (Heckert and Lucas, 2000b). During the Adamanian, very early in the evolution of dinosaurs, the fused tibia-fibula-astragalus-calcaneum that is the hallmark of derived ceratosaurs appears in *Camposaurus arizonensis* Hunt et al. (Lucas et al., 1992; Long and Murry, 1995; Hunt et al., 1998). By Revueltian time, ceratosaurs are marginally more abundant and, as the fossils described here demonstrate, have evolved into a body form classically identified as coelophysoid. Indeed, this design would prove so successful that it would remain essentially the same through the later evolution of *Coelophysis* and *Syntarsus rhodesiensis*, the latter of which would not become extinct until nearly 185 Ma. With the possible exception of some of the more plesiomorphic titanosaurid sauropods, no other group of dinosaurs has retained such a consistent body form for such a considerable (approximately 30 myr) span of time.

ACKNOWLEDGMENTS

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